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Introduction

This paper is an introduction to the biology and ecology of fungi in forest ecosystems. Examples of their interactions with other organisms are given so that the reader will gain a greater appreciation of the importance of fungi. Also included is a short discussion of the utility of fungi to people. The primary objective is to answer several questions. What is special about fungi? What do fungi do in the forest? And why should we care?

Unique features of fungi

Fungi are characterized by their microscopic threadlike cells called hyphae, and by production of spores. A group of hyphae is called mycelium. Mycelium tends to be immersed in a substrate, such as soil, wood or living plant tissues, that is both the surrounding physical environment and source of nutrients for the fungus. Mycelium is usually concealed from view and often long-lived.

Most fungi produce sporocarps (mushrooms, truffles, etc.) that tend to be ephemeral, seasonal, and annually variable. In other words, mushrooms can only be found for a short time during the year, in particular seasons, depending on the species of fungus, and not necessarily every year. Nonetheless, rarely can we identify fungi without their sporocarps. These characteristics are very different than higher plants, or even lichens, which can often be found and identified through much of the year.

Ecology of fungi

In thinking about the ecology of fungi, it is important to consider several phases of life history.

Various phases have different habitat requirements, occupy different physical locations, perform different functions, and experience different environmental conditions. For example, a portion of one mycelium may be in contact with root tissues, another portion inhabit the soil, and sporocarps be produced in yet another habitat, such as a rotting log. Studying the ecology and understanding the habitat needs of fungi is not a

simple task.

It is also hard to distinguish between individuals of a fungal species. Individual mycelia are concealed from view. Some individuals produce few sporocarps, others many, and sporocarps occurring close to each other may or may not be from the same mycelium. Conservation of any rare species requires an understanding of the dynamics of individuals and populations; we have much to learn if we are to apply these principles to fungi.

To many people, fungi conjure an image of decay and destruction. Although some fungi are pathogens and decomposers, they serve many other functions in the forest ecosystem. Fungi are part of a complex system that cycles matter and energy. Plants turn sunlight, water, nutrients and carbon dioxide into biomass; other organisms consume the plant tissues and cycle it back into CO2 and nutrients. Fungi have important roles in the forest canopy and soil where plants exchange materials with the atmosphere and soil.

1) Roles of fungi in the canopy.

Fungi in the forest canopy perform several functions. Bacteria are the only organisms capable of fixing atmospheric nitrogen, and some canopy lichens host these nitrogen-fixing bacteria. It is estimated that 10% of the nitrogen input to old growth Douglas-fir stands comes from such lichens. Most long-lived plants have fungi within their leaves known as leaf endophytes. Leaf endophytes occupy the interior spaces of leaves, but are not inside plant cells, and are normally present in healthy plant tissues. These endophytes can produce antibiotics or other substances that make leaves unpalatable to insects. Endophytic fungi may also deter pathogenic fungi.

Some fungi grow over the surface of leaves or twigs as epiphytes. Epiphytic fungi may deter pathogens and leaf-grazing insects. Another role for these fungi is in canopy food webs, where they serve as food for various organisms, particularly small arthropods. There are many defoliating insects in the forest, their populations held in check by predatory insects. Old growth forests have many times more predatory insects than do plantations, probably because of the abundance of small arthropods that the predators feed upon. The link between primary production and these predatory insects may include leaf epiphytic fungi, which serve as food for micro arthropods.

2) Roles of fungi on the forest floor.

The soil is where most fungi reside in the forest. A thimbleful of soil can have many meters of hyphae and thousands of species of fungi. Most of these species are micro fungi, which never produce mushrooms or other sporocarps. Fungi in the soil include decomposers, pathogens and mycorrhizal species.

Soil is, of course, the place where plants get their water and mineral nutrients, and fungi are involved in cycling dead material into usable nutrients. As fungi consume organic matter, they release nitrogen, phosphorus and other nutrients in the course of decomposition. Decomposition makes a contribution to forest health and should not be viewed only as the destruction of valuable wood.

Fungi can act as pathogens, but not only with negative impacts. Although pathogens can cause economic loss, from an ecosystem perspective they have many useful roles. In a closed-canopy stand, pathogens can cause large openings, called gaps, that provide the bright, sunny conditions required by early successional vegetation. This contributes to habitat diversity in the stand and allows it to support more wildlife species than closed-canopy stands. Trees killed by pathogens become snags and logs that serve as nests, perches and food sources for many birds and mammals.

Mycorrhizae

Mycorrhizae are symbiotic associations of fungi with the roots of plants. Douglas-fir root systems do not have "root hairs" in a natural environment -- the entire fine, feeder root surface is covered by a mantle of fungal tissue. Fungal tissues penetrate between outer cells of these feeder roots. Virtually all nutrients and water entering the plant are transferred through the fungal tissue. Most vascular plants depend on mycorrhizal fungi for nutrient uptake. In the forested portions of the Pacific Northwest, we have between 30-50 ectomycorrhizal host species, primarily in the pine, beech, birch and willow families; these species host several thousand species of fungi. Most other plant species form different kinds of mycorrhizae, and some are non-mycorrhizal.

Mycorrhizal fungi act as an extension of the root system. They penetrate the soil beyond the reach of roots, thereby increasing nutrient and water availability to plants. They also protect roots from some soil pathogens by acting as a physical barrier, and by producing antibiotics. Hyphae of mycorrhizal fungi can link plants of the same or different species. These linkages can transport the products of photosynthesis

from one plant to another, providing energy to help seedlings get established in the understory. A striking example of this in our forests are Indian pipes. Contrary to popular belief, these plants are not saprophytes. They rely on mycorrhizal fungi to get their energy, while the fungi in turn rely on green plants that are photosynthesizing. Indian pipes are more properly called myco-heterotrophs, not saprophytes.

Mycorrhizal fungi have effects on the biological, physical, and chemical structure of soil. Mycorrhizal fungi draw photosynthate (sugars) from their hosts; this sugar is transported away from the roots by hyphae extending into the soil. Some leakage occurs from the hyphae, and the fungal exudates glue soil particles together, forming aggregates. Aggregates are important in nutrient cycling because they are sites of microbial activity, and they increase soil aeration and water-holding capacity. Carbohydrate pumped into soil through the mycorrhizal hyphae also helps support the diverse microbial communities living there.

More than half of the micro arthropod species in soil are specialized fungal feeders.

Species of mycorrhizal fungi colonizing roots have a selective influence on associated soil organisms.

Communities of bacteria and protozoans vary depending on which fungus species is forming the mycorrhizae. Many free-living, nitrogen-fixing bacteria associate with particular fungal species.

Plants need water to photosynthesize. Mycorrhizal fungi aid plant water uptake by penetrating soil away from roots, thus exploiting water beyond the root zone. Hyphae also get water from small pores in the soil that are inaccessible to roots.

Mycorrhizal fungi are important in reforestation, especially on harsh sites with short growing seasons. To become established, seedlings require mycorrhizal fungi. When trees are removed in logging, the mycorrhizal fungi left there can survive for some time. If a site is too harsh, and no energy is provided for the underground ecosystem, mycorrhizal fungi die. Reforestation needs to happen within a window of opportunity, before changes in the underground ecosystem occur. The duration of the window of opportunity depends upon many factors, and is an active area of research.

Mycorrhizal fungi are also key players in plant succession. On glacial moraines in the Cascade Mountains, early colonization is by plant species that can either survive without mycorrhizae or form mycorrhizae with fungi that disperse their spores on the wind. Plants that depend on mycorrhizae that disperse spores with soil movement typically colonize later.

Food webs

Fungi also play a role in food webs. Sporocarps are food for many organisms, including slugs, insects and other arthropods, and mammals. Hyphae penetrating out into soil are also a source of food for other organisms such as bacteria, protozoa, and many types of invertebrates. In our region, the northern flying squirrel and red-backed vole are mycophagists (fungus feeders) almost exclusively, relying mostly on truffles. The northern flying squirrel is also the main prey of the spotted owl, so we can see a direct link between fungi and a federally listed endangered species. Efforts to create habitat for the spotted owl focus in part on flying squirrel populations and the effects of forest management on truffle production.

Sporocarps are consumed by squirrels, rodents, deer, elk, bears, and other mammals. Mushrooms are rich in certain amino acids and can be good protein source. Perhaps more important to wildlife are mineral salts that are concentrated in fungal tissues.

Animals also fall prey to fungi. The carpenter ant sometimes falls prey to a *Cordyceps* species, which colonizes the ant's body. Fungi are also consumed by other fungi. For example there is another *Cordyceps* species that parasitizes a truffle. This is interesting from an evolutionary point of view because *Cordyceps* have two major sorts of "hosts" insects (ants, beetles, butterflies) and truffles. These two unrelated groups of organisms both have chitin in their cell walls. It is interesting that *Cordyceps* has specialized on insects, and can switch to parasitizing truffles.

Importance of fungi

Fungi, with an estimated 1.5 million species, are the most diverse group of organisms after arthropods. Biodiversity is important because we need other organisms, including fungi to survive. The United States is a leader in legal protection of biodiversity. From the National Parks System, established in 1874, to the Endangered Species Act of 1970, and the National Forest Management Act of 1976, our nation has placed high value on our biological resources. The Northwest Forest Plan takes an unprecedented step in conservation of fungal diversity. Over half of the species requiring surveys or protection of known sites are macrofungi. The Bureau of Land Management and the Forest Service are now obligated to provide some level of protection to many fungi.

Protecting biodiversity is profitable. The multi-billion dollar pharmaceutical industry derives almost

all new drugs from chemicals originally isolated in nature, many of them from fungi. Some species of fungi have anti-cancer properties; although no drugs have been commercially marketed for this purpose yet, it is a promising area of research. Commercial harvest of mushrooms is a growing industry, and many people enjoy picking and eating wild mushrooms. Chanterelles, morels, and matsutake are the most abundantly harvested wild mushrooms. The impacts of harvesting on later mushroom production is another area of active research.

In summary, just as there is more to the forest than the trees, there is more to fungi than rot and mold. The functions of fungi in the forest are myriad and crucial to its health. For more information about fungi, see the references listed below.

References

Allen, M.F. 1991. The Ecology of Mycorrhizae. Cambridge University Press, New York. 184 pages.

C.J. Alexopolous, C.W. Mims, and M. Blackwell. 1995. Introductory Mycology, 4th ed. John Wiley and Sons. 880 pp.

Molina, R. and D. Pilze, eds. Managing Forest Ecosystems to Conserve Fungus Diversity and Sustain Wild Mushroom Harvests. USDA Forest Service General Technical Report PNW-GTR-371. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 104 p.

______, T. O'Dell, D. Luoma, M. Amaranthus, M. Castellano, K. Russell. 1993. Biology, ecology and social aspects of wild edible mushrooms in the forests of the Pacific Northwest: preface to managing commercial harvest. General Technical Report PNW-GTR-309. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 42 p.

Ouestions:

1. What happens to mycorrhizal fungi in situations where orchid species are lost because of timber sales? How long do those mycorrhizae take to return to where they can support some of these orchids?

Fungi will be impacted most by harvest of overstory trees, which are their source of photosynthate. Orchids may be associated with specific mycorrhizae; in terms of management impacts, we have almost no information on which species are most affected by timber harvest and how long they take to come back; experiments currently being done on different management practices/different levels of harvest could also look at the mycorrhizal component. But generally, there is very little information on this subject.

2. Is there a difference in diversity of fungi in terrestrial vs. saturated soils in wetlands?

There is a gradient of wet to dry sites where mycorrhizal fungi were studied; wet sites border on spruce, dry sites border on Douglas fir; wet sites had the lowest diversity of mycorrhizal fungi, especially of ectomycorrhizae. In wetlands, some fungi have adapted to this; but overall diversity is lower. Those adapted to wetlands are more rare.

- Is there a difference in fungi found in rangeland ecosystems compared to forests?
 Marcia will talk about rangelands but there is a very different set of players; partly influenced by vegetation and physical condition of the habitat.
- 4. After changes in a forest like clearcutting and fire and going from a mature forest stand to a shrub community, does fungi stay in soil and re-innoculate new plants, or does fungi change to a new group of species?

Who knows. Difficult, because until recently we have had to rely on macrofungi to identify the species present. But, using DNA and other techniques, we can now look at species on individual root tips and begin to address this question. However, molecular work is still time consuming. Preferably we would have to watch through the whole cycle, before stand is cut, and then determine if original species persist or if new species come in. So far, no conclusive data on this. For example, do some early-fruiting species (i.e. chanterelles) persist through logging, or do they need to be reintroduced?

5. What is the effect of soil compaction through trampling?
There is some evidence that compaction reduces diversity of mycorrhizae.

Hale, M.E., Jr. 1990. A synopsis of the lichen genus *Xanthoparmelia* (Vainio) Hale (Ascomycotina, Parmeliaceae). Smithsonian Contributions to Botany 74:1-250.

McCune, B., and R. Rosentreter. 1992. *Texosporium sancti-jacobi*, a rare western North American lichen. The Bryologist 95:(3)329-333.

_____, and T. Goward. 1995. Macrolichens of the Northern Rocky Mountains. Mad River Press, Eureka, California. 208 pp.

Rosentreter, R. 1993. Vagrant lichens of North America. The Bryologist 96:333-338.

_____. 1994. Displacement of rare plants by exotic grasses. Pages 170-175 *in*: S.B. Monsen and S.G. Kitchen, compilers. Proceedings - Symposium on the ecology and management of annual grasslands. Gen Tech. Rep. INT-GTR-313, USDA Forest Service, Intermountain Research Station, Ogden, UT.

Stenroos, S. 1990. Cladonia luteoalba - an enigmatic Cladonia. Karstenia 30:27-32.

Thell, A., T. Goward, T. Randlane, E.I. Karnefelt & A. Saag. 1995. A revision of the North American lichen genus Ahtiana (*Parmeliaceae*). The Bryologist 98:596-605.